THE GERM-PLASM HYPOTHESIS OF WEISMANN UNTENABLE.

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MANY scientists who have approached biology from the side of mathematics, physics and chemistry have injected the certainties of physical science into their explanation of the phenomena of life, a variable. In the foremost rank of philosophical biologists stands August Weismann, who is author of the most ingenious materialistic hypothesis offered to explain heredity and ontogeny. Weismann claims in his hypothesis that a very precious portion of germ-plasm, peculiar in its qualities to each species, is handed on from generation to generation, bearing impressed on the matter composing it the characteristics of parents to offspring. Shielded from rude contact with the external world, the qualities of the plasm change but slowly, just enough to carry forward the work of evolution.

Filled with admiration for the great atomic theory, in which the qualities of the molecule are said to depend upon the kind, number and arrangement of the atoms composing it, Weismann imagined that the germ-plasm must consist of myriads of tiny aggregations of molecules, which he decided to name biophors, or bearers of the qualities of life. These biophors must equal in number of kinds the total number of qualities exhibited by all plants and animals, one biophor for each quality. As there are many millions of such qualities, the disciples of Weismann match them with billions of biophors in each germ-cell.

Each biophor, Weismann imagined, could assimilate food, grow and divide so the total number would equal all the needs of all the cells of each individual. Weismann further imagined that the biophors became united into groups which he named determinants, there being one determinant for each cell of the body, except the germ-cells. The germ-cells must have all the different kinds of determinants needed by the developing plant or animal. But these determinants of the germ-cells could also absorb food, grow and divide as well as the biophors, so there would always be enough of them for all the cells of the body, no matter how many they might be. The determinants were thought to be somewhat piggish in their dispositions so they would struggle with one another for food and oxygen, and some would get more than their due share and grow faster and become dominant, while others would starve and

be recessive. These are certainly strange propensities for matter to exhibit.

Weismann has never seen a biophor nor a determinant, but imagines them to exist, just as the chemist imagines atoms to exist, never having seen them, because they enable him to offer a solution to a difficult problem. Weismann fails to note one serious difference between the condition of atoms in a molecule and that of molecules in a biophor or a determinant. Atoms are probably held by powerful polar forces to a definite arrangement in the molecule; but the molecules of biophors and determinants in a fluid, colloidal mass like protoplasm can have no such fixed arrangement. The few kinds of molecules in the rapidly multiplying chromatin granules or microsomes are in a constant state of flux of construction and destruction during the lifetime of every protoplasmic cell. Even if all proteids were crystalloids, this instability of molecular arrangement but proves the presence of an influence, such as life can exert, that can build or unmake crystals with a rapidity and ease unknown in all other crystalline substances.

Nutriment and oxygen must flow in a steady stream into the living cell, energy must be continuously liberated for the activities of the protoplasm, and useless matter must be as continuously excreted, or the cell dies. All this would seem to prove beyond question that the many kinds of molecules, their definite and stable arrangement in the biophors and determinants, required to give a physical basis to the germ-plasm hypothesis, are absent from living protoplasm. No known law of chemistry, no known law of physics, sanctions the statement that the arrangement of the molecules and supermolecules in colloidal matter like protoplasm can and does produce combinations possessing the characteristics of the biophors and determinants claimed by Weismann and his disciples.

But some disciple of Weismannism may say that the qualities exhibited by all the kinds of plants and animals may inhere, nevertheless, in some unknown way in the matter composing their bodies. Darwin and many others beside Weismann have imagined that this might be true. What are the possibilities for matter to play an important part in heredity? The qualities of the parents go in some way to the offspring. Either matter must possess and carry them or we must make an entity of that so-called quality of matter, termed life, and let it carry the inherited qualities. The second horn of the dilemma is the one which a rapidly increasing number of biologists have decided to take, and even Weismann admits that life may be the bearer of inherited characteristics from parents to

offspring (Evolution Theory, vol. II, page 369), but naturally prefers his own hypothesis.

Knowing the characteristics of life and the qualities of matter by personal experience and observation, we ought to reach a large measure of certainty as to which is the bearer of inherited qualities by making a careful study of the process of reproduction in plants and animals. The remainder of this paper will be devoted to a presentation of this process and to showing wherein the activities of organisms transcend all known powers and qualities of matter and energy, but are germane to a third entity, life, as capable of definition as are the other members of this triumvirate.

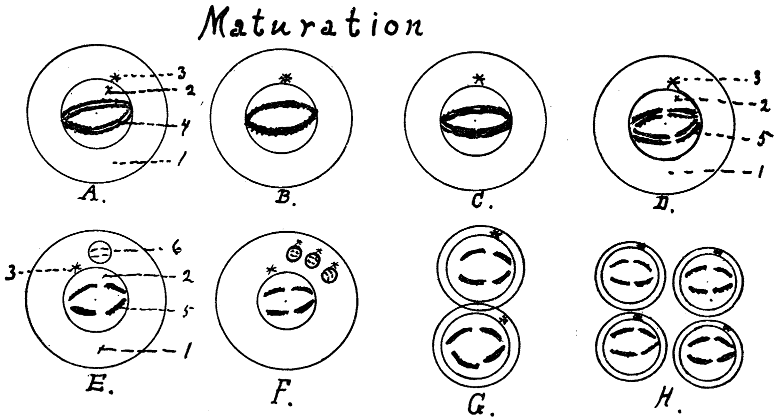
MATURATION.

A to *H*.—All protoplasmic cells of higher plants and animals consist of protoplasm of several kinds in form and function. In the outer part of the cell is the cytoplasm, *A*-1, concerned in the various processes of absorption, nutrition and excretion; and near the center of the cell, the nucleus, 2, possessing control over cell-conjugation and cell-division. The cytoplasm consists of a reticulum or spongioplasm in which, in plant-cells, are embedded numerous and variously colored plastids, nutritive in function, a fibrillar plasma which influences the process of development, and a structureless fluid, the hyaloplasm. Near the nucleus is an interesting body, the centrosome, 3, which plays a very important part in nuclear division in most animal cells and in the lower plants. The nucleus consists of a structureless fluid, the nucleoplasm, somewhat different from hyaloplasm, a reticulum holding one or more nucleoli of unknown use, a granular material which stains deeply, the chromatin, and fine fibers which for the most part do not stain at all, the linin.

At the beginning of the process of maturation the chromatin granules, sometimes called chromomeres or microsomes, arrange themselves, as though in obedience to some word of command, along two crinkly threads of linin. In the diagrams which illustrate this paper no attempt has been made to represent the actual appearance of these threads under the compound microscope, nor has any attempt been made to show the spindle of linin threads, which does such important work in cell-division. The two threads of linin along which the chromomeres have arranged themselves are the spiremes, 4.

It should be remembered at the outset that cytoplasm is derived from preëxisting cytoplasm, that nucleus is derived from preëxisting nucleus or nuclei; one does not make the other when it is ab-

sent and soon dies without it. Also, centrosome arises by division of centrosome, and plastid by division of plastid. The chloroplastids and chromoplastids are derived from leucoplastids. Evidently these forms of protoplasm would each occupy less and less space by self-division did they not absorb and assimilate nourishment and become more and more inactive did they not continuously release fresh supplies of energy from energy-containing foods for



the activities of the protoplasm; but all this is merely additional proof that in studying these forms of protoplasm we are studying the various manifestations of a power that is something more than that possessed by matter and an intelligence that is greater than that manifested by unharnessed energy.

The two spirem threads, shown in *A*, soon move together, chromomere of one moving to a chromomere of the other.* The result is a single spirem shown in *B*. This conjugation persists in the case of *Lilium canadense* for from two or three days to a week. What happens while the two threads are in conjugation, what influences cross from one chromomere to the other, no one knows. The best observers believe that the conjugating chromomeres of the two spirems come from different parents, those of one spirem from one parent and those of the other spirem from the other. During the lifetime of the individual producing the mother germ-cell, the chromomeres remained distinct, and all the cells of her body were under the control of those chromomeres whose life powers were dominant, according to the Mendelian law.

After close union for several days the spirem splits, as shown in *C*, but no one knows whether the division plane corresponds to the

*This description follows somewhat closely that of chromosome reduction in *Lilium canadense* by Charles E. Allen, University of Wisconsin, in *Botanical Gazette*, June, 1904; and of Strasburger and Lang, 1908.

previous plane of union or not. Then in a short time the two spirems divide transversely, shown in *D*, into segments termed chromosomes.

In the mother germ-cells of many species of plants and animals, the two spirem threads divide transversely, before union, into chromosomes. These unite, chromosome with chromosome, chromomere with chromomere, remain in close union for several days, and then separate, as do the spirem threads. From either method of union and division there always results a definite number of chromosomes peculiar to the species. In this case the number eight has been taken, shown in *D*. Every species of plant and animal has its peculiar number. In certain red algæ there are 40 chromosomes; in sharks, 36; in certain gasteropods, 32; in the salamander, trout, mouse, fern, lily and man, 24; in the sagitta, ox, guinea-pig and onion, 16; in the grasshopper, 12; in a liverwort, 8; and in some of the nematodes, 8, 4 or 2.

The mother egg and mother sperm-cells of the same species of plant or animal have the same number of chromosomes in their nuclei. These mother germ-cells differ in appearance chiefly in their form and in the amount of cytoplasm they contain, the mother egg having even many thousand times as much cytoplasm as the mother sperm.

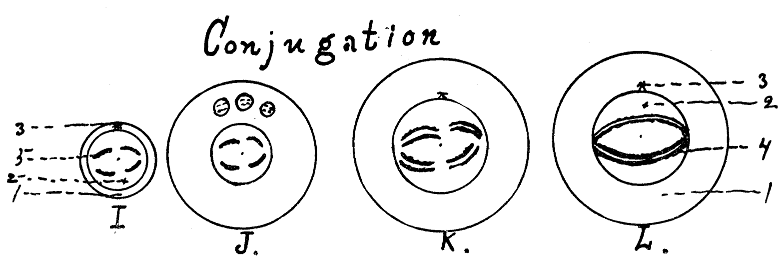
In *animals* before the egg and sperm are ready to conjugate the mother egg and the mother sperm nuclei must each reduce the number of chromosomes one-half. In the mother egg-cell, as shown in *E* and *F*, the nucleus has divided unequally by mitosis and four of the chromosomes have passed out into the cytoplasm with a small part of the nucleoplasm, becoming the first polar body, *E*-6. Actuated by a very primitive instinct, the chromosomes of the nucleus and the polar body split, and each nucleus divides by mitosis, the former unequally as before, and the latter equally. The result is shown in *F*. In a similar way the mother sperm-cell divides by mitosis into daughter sperm-cells and these into granddaughter sperm-cells or sperms, again making four resultant cells according to the primitive instinct. It will be noted in *G* and *H* that the mother sperm-cell divided equally, making four functional sperms, while the mother egg-cell, by dividing unequally, produced only one functional egg. The three polar bodies may perhaps assist in organizing the cytoplasm for the work of preparing nutrition for the embryo.

In *plants* the process of maturation is the same as in animals, except that the resulting cells are not eggs and sperms, but *spores*,

which must germinate and produce another organism whose cells have half the normal number of chromosomes, and which finally produces eggs and sperms in peculiar organs. Plants which produce spores of equal size are isosporous, and plants which produce spores of unequal size are heterosporous, the large spores being named megaspores and the small spores microspores. The liverworts, mosses and common ferns are isosporous; and marsilia, selaginella, the pines and spruces, and all our common flowering plants produce spores of different sizes and are therefore heterosporous.

CONJUGATION.

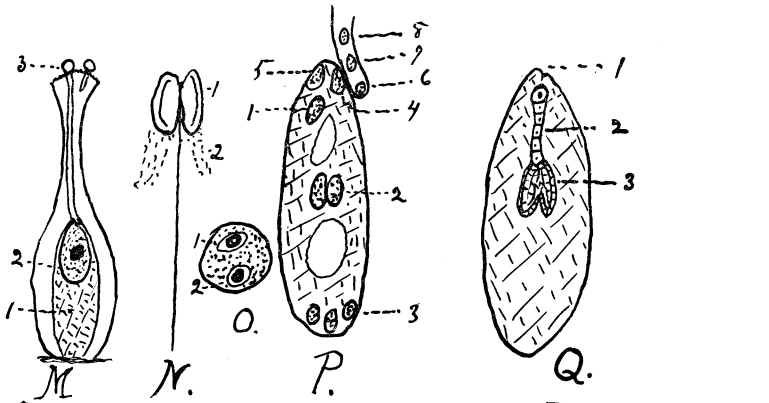
I to *L*.—On the conjugation of one of the sperm-cells with the egg-cell, complete fusion of the cytoplasm and nucleoplasm takes place, but the chromosomes do not unite but continue distinct during myriads of succeeding cell divisions till the next period of maturation. The three polar bodies of the egg-cell disappear as does also its centrosome, the centrosome of the sperm-cell officiating



in the cell divisions. It will be noted in *K* that the fertilized egg has eight chromosomes, and that finally these unite to form two spirems, shown in *L*, at the beginning of the next maturation after myriads of cell divisions. The process of conjugation of eggs and sperms is the same in plants and animals.

PLANT FERTILIZATION AND EMBRYOLOGY.

M to *Q*.—It has long been known that the spore-containing organs of plants are usually modified leaves. Gray long ago taught that the simple pistil is a leaf so modified that it forms a closed chamber or cell in which the ovules (megasporangia) are developed along its united margins. We know that the embryo-sacs of the ovules are megaspores, that the ovules are megasporangia, and that the pistils are megasporophylls. In like manner the stamens, usually modified leaves, are now called microsporophylls; the anthers, microsporangia, and the pollen grains, microspores. In diagram *M*, 1 is the nucellus containing the embryo-sac, 2; and 3 is a pollen



Plant Fertilization & Embryology

grain germinating on the stigma. *N* represents a stamen with its filament, anthers and pollen. *O* is an enlarged pollen grain or microspore. Among mossès when certain spores germinate there are developed plants of considerable size with rhizoids, stems, leaves and sperm-producing bodies, the antheridia; and other spores develop into similar plants with egg-producing organs, the archegonia. Such organisms are known to the botanists as the male and female gametophytes; and among mosses they are the chief food-elaborating structures. But among flowering plants, the cottonwood, for example, the sperm- and egg-producing gametophytes have degenerated till only a few cells remain, and the organisms are entirely dependent on food stored in the spore by the parent sporophyte. The germinating microspore of the cottonwood shows only two or three gametophyte cells, viz., a tube-producing nucleus, *O*-2, and a mother sperm-cell, *O*-1.

It will be remembered that when the animal mother germ-cells mature (see diagrams *F* and *H*), one functional egg nucleus is produced and four functional sperms; but the botanist has found that in plants these germ-cells are all spores. Among mosses and common ferns all the spores are equal in size and each may develop, so far as the botanist knows, into a male or a female gametophyte; or in some species the spore develops into a gametophyte which bears both kinds of sexual organs, the antheridia and archegonia, containing at maturity respectively the sperms and eggs. In marsilia, selaginella, the gymnosperms and the angiosperms, the spores produced by the maturing mother germ-cells are of unequal sizes, and are therefore named microspores and megaspores. The

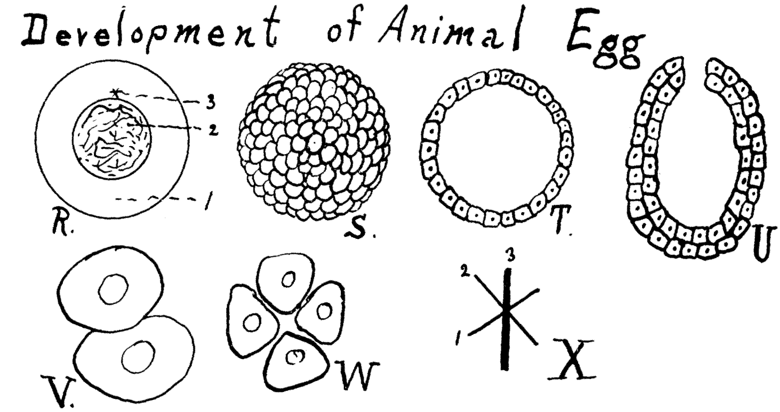
microspores always produce, on germination, male gametophytes, and the megaspores female gametophytes.

In the megasporangium (ovule) of the canna four megaspores develop, according to the ancient instinct, but only one is functional. In most angiosperms, including the cottonwood, only one megaspore reaches any size. This megaspore, shown in *P*, contains at first only one nucleus. This nucleus soon divides in rapid succession till eight nuclei are formed, four at each end of the megaspore or embryo-sac. Then one of each four moves to the middle of the sac and there the two fuse to make the polar nucleus, *P*-2. Of the three nuclei which remain near the micropylar end of the sac, 4 and 5 are synergids or helpers, and 1 functions as egg. The three nuclei at the distal end of the sac are the antipodal nuclei, 3, and are believed to represent a few of the cells of the degenerate female gametophyte. Possibly the synergids, 4 and 5, represent an archegonium.

When the pollen (microspore) tube reaches the vicinity of the embryo-sac, the tube nucleus, 6, disintegrates, and the mother sperm nucleus divides into two sperms, 7 and 8. Synergid 4 disappears and one sperm nucleus, 7, passes into the sac, makes its way to the polar nucleus, 2, and unites with it, forming the endosperm nucleus which has charge of providing nourishment for the embryo. Sperm nucleus 8 enters the sac and unites with the egg. The fertilized egg at once takes nourishment and divides repeatedly. True to an ancient instinct, it so divides at first as to make a filament, as is still the only or chief method of the algæ. This filament, the suspensor, *Q*-2, serves to push the rapidly growing embryo, *Q* 3, into the food stored in the endosperm. *Q*-1 represents the location of the micropyle. How can any one compel his mind, even though it be steeped in physics and chemistry — how can any one believe that this wonderful process of fertilization and development is merely a function of matter?

DEVELOPMENT OF THE ANIMAL EGG.

R to *X*.—The fertilized animal egg consists usually of a large amount of cytoplasm, *R*-1, a nucleus which contains chromatin, *R*-2, which becomes organized into the normal number of chromosomes when the cell is preparing to divide, and a centrosome, *R*-3. The fertilized egg-cell of animals divides and redivides in a fashion peculiar to animals. The first divisions are in the three planes at right angles to one another, *X*-1, 2, 3, making first two cells, *V*, four cells, *W*, then eight, sixteen and thirty-two cells arranged in a solid sphere or morula. As the next step in development a cavity ap-



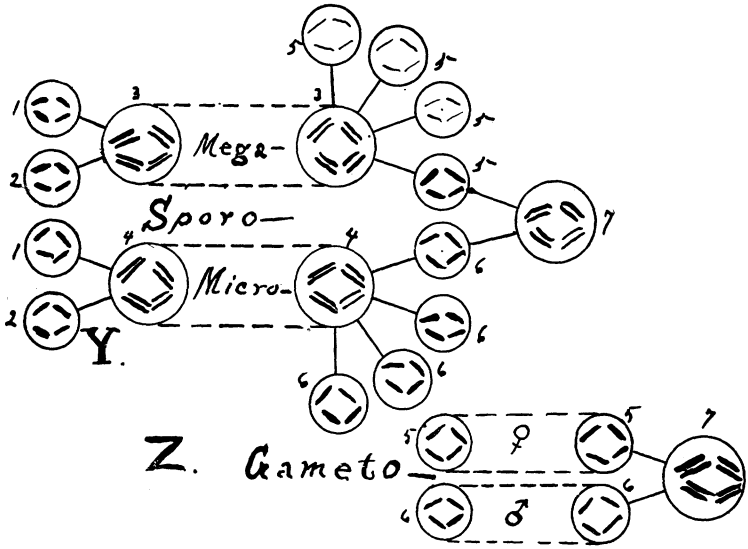
pears in the solid sphere, the cells multiply rapidly and the embryo becomes a blastula, *S* and *T*. The third stage in development, shown in section in *U*, is that known as the gastrula, produced in various ways, but usually by the invagination of one side of the blastula, due to unequal cell division and growth. The gastrula may be likened to a two-walled cup with a small mouth. In some form or another all complex animals pass through this stage of development, as well as the morula and blastula stages. After the gastrula stage is reached animal bodies of the highest complexity are produced by a series of simple and compound invaginations and evaginations, tubular or furrow in shape and many times repeated, involving the ectoderm, entoderm and mesoderm.

SUMMARY OF REPRODUCTION IN PLANTS AND ANIMALS.

Y and *Z*.—Diagram *Y* illustrates reproduction in animals, but *Y* and *Z* are both required to illustrate the same in plants. It should also be noted that in all cases when egg and sperm unite it cannot be foretold whether the resulting individual will in the case of animals produce eggs or sperms, or in the case of plants produce spores that will develop into male or female gametophytes.

For *animals*, in diagram *Y*, we will suppose that two sperms, 1, 1, unite with two eggs, 2, 2, each cell having a nucleus with four chromosomes; the resulting fertilized eggs, 3, 4, will each have eight chromosomes. Let us suppose that the fertilized eggs produce two individuals, one female, 3, 3, and one male, 4, 4. When the female produces one functional egg, 5, and the male four functional sperms, 6, 6, 6, 6, the cycle will be complete.

For *plants*, in diagrams *Y* and *Z*, the process of reproduction is the same as that indicated in diagram *Y*, except that one functional spore capable of developing into a female gametophyte is produced,



and four functional spores capable of producing male gametophytes are produced. In most of the higher plants the former is a megaspore and the latter are microspores. The cycle for plants is completed when the megaspore germinates and produces a female gametophyte, 5, 5, which bears an archegonium containing, when it matures, an egg, and the microspores germinate and develop into male gametophytes, 6, 6, bearing antheridia containing at maturity the sperms; 7 and 7 are merely fertilized eggs, like 3 and 4 at the left in diagram *Y*, the upper 7 for animals and the lower 7 for plants.

Weismann invented his hypothesis respecting the continuity of germ-plasm to combat the hypothesis of Lamarck that acquired characters are inherited. Weismann contended that the cells of the body may be grouped into two classes, the soma- or body-cells and the germ-cells. He declared that the soma-cells might be modified by use, but such modifications could not be transmitted to offspring, for the germ-cells would remain unmodified.

This ingenious hypothesis was at once attacked by the Lamarckians and Neo-Lamarckians, and Weismann added biophors and determinants to his germ-plasm to strengthen his position.

Many mathematical biologists have accepted Weismann's views respecting heredity, and have declared that Lamarckianism is dead. If they are right, it is very strange that the disciples of Weismann are obliged to repeat their declaration so frequently.

The two main assertions of Weismann have not been proved.

He has not proved that germ-plasm is handed on from generation to generation little changed, nor has he shown that life is a quality of matter due to the number, kinds and arrangement of supermolecules called biophors and determinants.

It is well known, on the contrary, that germ-plasm and all other forms of protoplasm are undergoing continuous change through oxidation and repair of waste and through growth and division of cells, millions of times repeated in the case of the germ-cells, especially. Each plant and animal produces during its lifetime, if it matures, thousands up to many millions of germ-cells. The plasm with which each organism began would be but as a drop of water to a barrelful compared with what it sends out. Nor can life be merely a quality of matter due to the number, kinds and arrangement of supermolecules in a colloidal mass of matter, containing few kinds of molecules and undergoing constant change through nutrition, oxidation and excretion.

Such a claim for matter is so remarkable that a full statement of its significance will show best how foreign such qualities are to the matter of science and how appropriate they are to matter of the imagination. Let us consider four facts universally known to be true of organisms: (1) Since there are about one million species of plants and animals on earth to-day, and at least twenty-five million have existed in prehistoric times; (2) since each species is represented by millions of individuals, and has in past times been represented by millions more, each with its personal characteristics; (3) since each complex organism has thousands up to billions of cells, which differ in their powers and functions; (4) since each organism varies from year to year, and each species varies from century to century: It follows that figures are entirely inadequate to express the number of combinations and variety of combinations of molecules and supermolecules that would be needed to provide a setting for these qualities, were such attributes possible to matter.

The molecules of lifeless matter may be shifted and rearranged at pleasure without showing in the least the qualities of living matter; and no chemist or physicist has yet been able to make even an organic molecule like starch from carbondioxid, water and sunshine, still less a supermolecule with life.

All true biologists must claim that a peculiar entity which he knows as life bears the myriad and variable qualities such as living organisms possess, and must sharply differentiate the powers of life from those of energy and matter. Matter alone, nor matter with energy, certainly cannot manage such complex reproductive processes as those we have just studied.

The writer of this paper believes that Weismann's hypothesis is fundamentally wrong. Life, not matter, bears inherited qualities. Life manages matter through energy for its own convenience while developing its powers. Life as we know it is not bounded by cell-walls but pervades the whole body in a general way, and provides for itself special lines of communication along nerve-fibers to control those parts which do work instinctively. The generative cells and the conscious powers are in especially close communication.

The first activity of the first organism must have been consciously performed. The nature of life is and was such that repetition bred habits, and habits persisted in for many generations became instincts and were then hereditary.

This body of instincts recruited from habits became in the simple and more complex organisms a great conserving influence, and prevented sudden change of method of living and doing. Body-building instincts, as all know, can seldom be entirely obliterated. The human embryo still has gills. Such instincts can be buried beneath better ones, but can seldom be destroyed.

So conscious activities in highly organized beings like man can do little to modify the growth of the body in its more primitive parts, and are powerful chiefly in directing the growth of the parts lately acquired, like the mammalian brain and the voluntary muscles. But all parts of the body can be modified through the effects of use and disuse, for a persistence on the part of life of the use or disuse of tissues and organs recently or long established, because of a permanently changed environment or habit of life, continued for many generations, has certainly resulted in a modification of the body-building instincts. Animals found in caves are minus eyes but possess greatly enlarged touch organs. Water-animals that have acquired the land habit, like the lung fish; snakes that have lost their limbs through disuse; land animals, like the whale and seal, that have become adapted to the water life, and many series of fossil forms, all prove the potency of life to change the body when the need arises. The germ-cells are intimately connected with the soma cells in a general way by a sort of wireless telegraphy and specifically by means of countless nerve-fibers. This intimate association is shown unmistakably in young animals when the removal of a portion of the germinal tissues is followed by a great change in the development of the rest of the body, and by the great influence of the mind and body over the germ-plasm during every moment of the maturing life of the individual.

But where is your certainty that life has made and can make such body-transforming volitions? asks, in substance, a leading

zoölogist. These body-transformations of lower organisms have not been established by man-made mutilations; environments cannot of themselves produce inheritable modifications; the only efficient agent, therefore, is the life within the organism. As to certainty, so long as life is a variable, so long as life is a law unto itself, we must reply that certainty in the very nature of the case cannot exist. He alone who has within himself the spirit of discernment of what life has done can exercise the spirit of prophecy and foretell what life may do; he must be in very truth a biologist, and not be heavily tinctured with the formalism of the mathematician, the physicist and the chemist.

Whether the inheritance of acquired characters shall result in an orthogenetic, saltatory or rameal evolution of a race depends on the many small, conscious choices of many lives, made in few or many generations, to better meet the conditions of a changing environment.

In conclusion, then, it is necessary merely to reaffirm what has been several times stated in this paper. The Weismann hypothesis is clearly untenable, for it is life that carries and transmits inherited characters and that compels matter to obey it through energy.